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The Significance of the Mychorrhiza of Pinus radiata

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FOREWORD.

During the summer season in Southern Australia when the soil becomes very dry, the fine surface rootlets of Monterey Pine become desiccated and apparently die. When the autumn rains have wet the soil these withered rootlets recover and put out white growing tips. Mr. Cromer in the course of a study of the water relations of this Pine found that Micorrhiza play a very important part. In this paper he describes the work done, traces the connexion between the root and the Micorrhiza and advances a theory for the hitherto unexplained revitalization of the apparently dead rootlets.

The paper will I hope inspire other foresters to examine the question ; much work remains to be done ; and on the fundamental side one may point to—1. the growing of the fungus in pure culture until fruiting bodies develop, and 2. the culture and inoculation and development of the fungus on a new host.

Mr. Cromer's work was carried out under the aegis of the University of Adelaide and, with its consent, is being published by the Commonwealth Forestry Bureau in accordance with its policy of printing the work of alumni of the Australian Forestry School.

C. E. LANE POOLE,
Inspector-General of Forests.

21st May, 1935.

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THE SIGNIFICANCE OF THE MYCORRHIZA OF PINUS RADIATA.

I. INTRODUCTION.

While engaged upon a study of the minimum water requirements of *Pinus radiata* at Kuitpo, South Australia, which entailed periodic measurements of soil moisture contents, the writer was confronted with the question of the part played by mycorrhiza in the absorption of water from the soil.

It has frequently been observed that in spite of the abundance of mycorrhizal infection the pine remains exceedingly healthy and is capable of vigorous growth. Indeed Kessell (1926) has attributed the poor growth of seedlings in new nurseries to the absence of mycorrhiza and has obtained superior growth by inoculation.

Controversy has been rife for some decades as to the nature of the association between the fungus and its host. Opinions of workers on this subject range from that of pure parasitism to the conviction of beneficial symbiosis of vital importance. Rayner (1927) has pithily expressed it thus—" In respect to the significance of mycorrhizs in trees, it may be recalled that every imaginable view has found supporters ".

All have concerned themselves with the question of nutrition, although reference has been made of necessity to the absorption of water. Pessin (1928) quotes Melin as suggesting that the mycorrhiza may replace the root hairs in the transference of water and salts to the roots, but explains that this does not mean that they may do so more efficiently than the root hairs.

This paper is intended to throw further light on the vexed question of the significance of the relationship.

II. COMMENT ON PREVIOUS WORK.

It is not proposed to include here an historical review. Such may be found in a paper by Masui (1927) and a brief broad outline has been prepared by Rayner (1929 and 1930). Many of the original papers are not readily accessible, but this is largely mitigated by the wealth of information gathered by Dr. Rayner and set out in her book *Mycorrhiza* (1927). All vascular plants and bryophytes are treated, the subject being arranged in historical sequence. One chapter is devoted to the ectotrophic mycorrhizas of trees, and another to a discussion of the physiological and nutritive significance.

The excellent work of Melin (1917–1925) which provided reliable and conclusive evidence of the nature, constitution, and identity of ectotrophic mycorrhizas is given in some detail. From cultural syntheses, field observations and anatomical studies Melin (1925) was led to the conclusion that mycorrhizal fungi facilitate the intake of ammonium salts and other organic compounds by the tree. Inorganic mineral salts are absorbed with equal ease by both infected and uninfected roots.

It will not be out of place however, to quote briefly Rayner's summary of present knowledge with regard to the mycorrhiza of trees.

1. Mycorrhiza is a constant feature of woodland soils and the fungi are mainly saprophytic genera.

2. The ectendotrophic habit prevails.

3. Normal mycorrhiza is developed only in a suitable rooting medium. Cultures make feeble growth apart from their hosts.

4. Under adverse conditions the root is not subject to a more intense attack.

5. The fungi profit from the association. They show stimulation, attributed to phosphatid exudates. There can be little doubt that they obtain carbohydrates from their hosts.

6. The presence of an investing sheath of mycelium about the absorbing region of the root offers no hindrance to the passage inwards of water and dissolved substances.

7. Inorganic salts are taken up as efficiently by infected as uninfected roots.

8. The fungi are able to utilize complex nitrogenous substances more readily.

9. In the plant world the severity of the struggle for existence not uncommonly centres about the competition for suitable compounds of nitrogen. It is not unreasonable to believe that the intimate association with fungus mycelium so common in all groups of vascular plants is but another manifestation of the urgency of this nitrogen problem among plants. In at least two of the three groups of mycorrhizal plants for which experimental data are now available, namely, forest trees and members of the *Ericaceae*, modern work has yielded corroborative evidence that this is actually the case.

10. There can be no doubt that recent investigations by means of pure cultures have tended to support the view that the possession of mycorrhiza is frequently of benefit to the vascular hosts, the nature and extent of such benefit depending upon the physical conditions of the environment and the physiology of the association in individual cases.

Since the publication of Rayner's *Mycorrhiza*, the most important paper is the third of a series by Masui (1927) which further supports the conclusions already drawn. It is emphasized that two groups of fungi exist, namely, facultative and obligate symbionts. The former does not necessarily require the association of tree roots, while in the latter case it is essential. In his first paper Masui (1926) worked on the association between *Cantharellus floccosus* and *Abies firma*. This fungus is an obligate mycorrhiza former and led Masui to support McDougall in his viewpoint of pure parasitism. Subsequently further biochemical research with a large number of different species revealed the fact that facultative mycorrhizas, such as *Boletus* while absorbing certain nutrients (amino-acids and sugar) were able to supply others (phosphorus) to the root. Masui denoted them as hemisymbionts doubtless meaning, hemi-beneficial symbionts in the strict sense of the word. Syntheses of several mycorrhizas in pure culture were also accomplished.

McDougall (1928) and McDougall and Jacobs (1927) have also published papers in which it is still insisted " that the fungus is a parasite on the root and derives food from it but that the root receives no benefit and may be injured by the relationship ".

Pessin (1928) sides with Melin, solely on the grounds of the vigorous condition of the affected seedlings.

Eardley (1932) described the mycorrhiza of *Pinus radiata* in South Australia in an unpublished paper. An endeavour was made to correlate the infection with Boletus granulatus by inoculation of sterilized pots. The uninoculated control pots contained mycorrhiza but a smaller amount than the remainder. Synthesis was also attempted.

III. THE NATURE OF MYCORRHIZA.

1. Relation to the Normal Root.

For an understanding of the significance of mycorrhiza it is necessary to consider basicly the nature of the root itself and also the relation of the fungus to this structure.

The normal young root of the pine has a central cylinder comprising the vascular tissue and pericycle, surrounded by the endodermis. Outside this is a large mass of cortical tissue bordered by the epidermis. The latter is composed of smaller cells than those of the cortex bearing occasional root hairs.

As development proceeds the central cylinder enlarges, the vascular tissue differentiates and the cortex cells which were formerly hyaline become stained brown with tannic substances (Masui 1926). Finally a cambium arises in the pericycle producing cork cells on its outer surface and the cortex is lost. At this stage we have the ordinary secondarily thickened root.

The mycelium of the mycorrhizal fungus infects the cortex only of the root and is in consequence intimately associated with the growing rootlet, as the cortex is not retained after a certain time.

Masui (1926, 1927) and others have shown that the effect of the fungus is to inhibit the growth of the infected rootlets. The majority of rootlets once infected do not form lateral roots but undergo modifications of structure to form mycorrhizas. The differences in structure of a fungus root have been set out by Laing (1932) as follows :—

(1) The number of cortical cells is less and the cells are larger.
(2) There are no resin canals subtending the primary xylem.
(3) The primary xylem is small in amount.
(4) Cork formation does not take place.

The same author has shown that the fungus gradually destroys the rootlet by encircling and isolating the cortical cells, and thus acts as a root pruner.

In this study the behaviour of the normal root was examined paradoxically under abnormal conditions in order to reduce the effect of fungal infection.

A large mound of subsoil was raised in the autumn. This soil was more or less free from mycelium and the growth of the roots was practically unhampered by any mycorrhizal infection over the short period of observation. The result upon examination in summer was very marked. Each axial root had produced great numbers of vigorous and long laterals bearing root hairs. This was in direct contrast to roots in the adjacent surface soil which contained few laterals, a scarcity of root hairs and numbers of mycorrhizal rootlets. This supports the view that root growth is diminished by fungal infection, a fact which has been stressed by Masui (1926).

Thus the infected root system instead of being a much branched structure consists of a long main root with an occasional vigorous lateral (which has escaped suppression) and numerous mycorrhizal rootlets replacing the remaining laterals.

2. EXTERNAL APPEARANCE.

The association between the roots of a specific tree and the mycelium of a specific fungus may adopt more than one form. Further, a given fungus may produce mycorrhiza with more than one tree. Consequently general description becomes a matter of some difficulty.

Melin's descriptive work has been set out by Rayner (1927). He outlines three main forms—

(1) Crowded dichotomous branching.
(2) The development of tubers from the fusion of form. (1) ?
(3) Simple unbranched structures.

but suggests that the form adopted may be only an indication of the " Virulence " of the root fungus under the existing conditions.

The commonest form to be observed on pines is the dichotomously-branched (one or more times) type which is shown by *Pinus radiata*.

3. CHARACTERS.

The infection may adopt one of the following four forms although it must be borne in mind "that there is no sharp distinction between the ectotrophic and endotrophic types of structure" (Rayner 1927) and further that the various forms may be yet another indication of the "Virulence" of the association (Melin—*see* Rayner 1927).

1. Ectotrophic.—The mycelium is external and no penetration of the cells occurs. This is a common form of tree mycorrhiza.

2. Ectendotrophic.—Penetration of the cells occurs in addition to the ectotrophic mycelium. Also common.

3. Heterotrophic.—A term originally suggested by McDougall (1922), refuted by Melin and supported by Masui (1927) to signify that the internal filaments are not ultimately dissolved away as in the ectendotrophic type. This is less usual.

4. Endotrophic.—The infection is entirely internal. It is doubtful if this form occurs in trees except as a developmental stage to (2) and (3).

The mycorrhizal rootlet is observed to be surrounded by a layer of mycelial tissue known as the mantle, which is composed of mycelial filaments variously fused together. Ectotrophic forms possess a mantle only which is compact, in close contact with the cortex, and effectively prevents the operation of root hairs. Ectendotrophic forms possess in addition to the mantle filaments which penetrate both inter and intra-cellularly. Such filaments dissolve away the cell walls which they contact and pass into the cells. Further many of the intercellular spaces may be filled with small fungal cells forming what is known as the "Hartig net".

The mantle gives off various hyphae and hyphal strands.

4. FUNGUS.

Of the fungi which form mycorrhiza nearly all are Basidiomycetes. The fruiting bodies are a familiar sight under any stand of conifers. The mycelium of a facultative mycorrhiza former is ramified through the soil and spore bodies may be formed from local concentrations on humus, &c. Roots growing through soil in this condition are not likely to escape contact with the mycelium. On the other hand the mycelium of an obligate mycorrhiza former is not capable of sustained existence unless contact with a root is made. Consequently the chance of infection is less.

The spore bodies arise in a number of ways, the chief of which is from the massing of numerous hyphal strands originating from infected roots (Masui 1926) or from the mycelium itself of a facultative mycorrhiza former.

5. SEASON AND CONDITIONS OF GROWTH.

It has been shown that it is the young absorbing roots which become mycorrhizas and the evidence suggests that the season of growth of the latter is simply governed by the seasonal growth of the roots (Masui 1927).

Melin has observed two periods corresponding with two maxima in the root growth.

Where an annually recurring season has been stated this is probably due to a single period of root development.

The formation of mycorrhizas is restricted to the surface layers of the soil (Masui 1926) the fungus mycelium being apparently unable to penetrate to any great depth.

The mycorrhizal fungus is very sensitive to the P H. value of the soil. Rayner (1927) quotes several authorities in support of optimum conditions between P H. 4.0 and 5.0.

The " virulence " of the association as postulated by Melin is largely controlled by the condition of the rooting medium (Rayner 1930). What soil conditions are necessary for optimum growth has not yet been determined, but as Rayner (1929) states " The types of soil most favorable to the growth of seedling pines promote likewise an easy and profuse development of mycorrhiza of the true mutualistic type.

IV. THE MYCORRHIZA OF PINUS RADIATA.

1. Fungus.

The fungus concerned in the relationship with the roots of monterey pine has never been conclusively determined. It is quite possible that more than one species is involved.

One Basidiomycete is very prevalent under stands of *P. radiata* throughout Australia, namely Boletus granulatus L., and suggests itself as the major mycorrhiza former in view of the fact that few other fungi are present in so conspicuous a quantity over such a wide range.

The Boleti are facultative mycorrhiza formers and consequently can exist and produce fruiting bodies independantly of pine roots. Such fruiting bodies when carefully unearthed at the base are not associated with roots but are formed from a mycelial network on decaying vegetable matter. They are sometimes formed however, from interwoven strands of hyphae projected from the mantles of several mycorrhizas. A fruiting body of the latter type has been photographed to show the origin of the strands (Plate 1). The familiar spore body is of the mushroom type, of a brownish yellow colour above and light yellow on the under surface.

That Boletus granulatus is responsible for mycorrhiza formation on the roots of monterey pine is suggested from the following facts :—

(1) B. granulatus is extremely prevalent in pine plantations.

(2) Mycorrhiza is likewise abundant.

(3) Few other fungi are so widespread.

(4 Direct connexion has been established by hyphal strands between mycorrhizal rootlets and the fruiting body. When pulled apart and examined microscopically the strands were found to have carried away the mantle and portion of the cortex with them.

Laing (1932) gives the following methods of identifying the fungi responsible for mycorrhiza formation :—

(1) To grow in pure culture hyphae isolated from a mycorrhiza until the fruiting bodies by which the fungus can be identified develop.

(2) To grow pure cultures of hyphae from the spores of fruiting bodies of fungi found near the roots of a certain tree and then to test by inoculation of the same or other tree roots if the hyphae so obtained can induce mycorrhiza formation.

(3) To trace connexions between tree roots and the fruiting bodies of fungi in their neighbourhood.

Of these the third was the most successful method. Microscopic examination showed that the hyphae of the mycorrhizas passed directly into the fruiting bodies.

This method has been used with success in the case of *P. radiata* and *B. granulatus*. Confirmation could be obtained from the synthesis of mycorrhiza in pure cultures of these species. In this connexion the following syntheses have been accomplished :—

Boletus bovinus—*Pinus densiflora*—Masui.
Boletus luteus.
Boletus variegatus—*Pinus montana*—Melin.
Boletus badius.
Boletus granulatus.

It is expected that such a synthesis will be possible between *Boletus granulatus* and *Pinus radiata*, although Miss Eardley (1932) has been unsuccessful as yet in bringing it about.

2. MYCORRHIZA.

1. *External Appearance.*

The mycorrhizal rootlet in external view is usually a short forked structure from 4 to 10 mms. long. The monopodial form is often present as well as the once dichotomously branched. Where conditions are favorable to their growth mycorrhizas occur in large numbers along the root to the exclusion of normal lateral roots. When young they are usually whitish in colour particularly in dry soil. The mycorrhizas darken with age and are almost black at death. The typical form is shown by plates V. and VI.

2. *Microscopic Features.*

(*a*) *Mantle.*—The most conspicuous feature of a microscopic section of the mycorrhiza is the presence of a mantle surrounding the cortex, similar to that described by previous workers (Masui 1926—Pessin 1928, &c.). The mantle tissue is white in colour and more or less indefinite in structure being composed of mycelial filaments matted and fused together. The thickness of the mantle varies but is seldom as thick as the cortex and can easily be distinguished from the latter which is brownish due to the presence of tannic substances. From the mantle are given off hyphae, and hyphal strands which are similar in appearance to the mantle tissue and branch freely.

(*b*) *Endotrophic Filaments.*—In addition to the mantle the mycorrhiza possesses endotrophic filaments which penetrate and often fill the cortex cells. Inter cellular filaments are also present and the chain-like "Hartig net". A photomicrograph of a hand section of cortex is shown by Plate II.

The mycorrhiza is therefore of the ectendotrophic or heterotrophic type. The cortex cells of old mycorrhizas with well developed mantles are sometimes unusually free from endotrophic filaments and the writer inclines to the view that they have become absorbed by the cells and that the mycelium is ectendotrophic.

(*c*) *Mode of Infection.*—In the soil described below which is particularly favorable to the growth of mycorrhiza the writer collected numerous root tips apparently unaffected. Microscopic examination, however, revealed that in all cases roots were infected within 2 inches of the end. Indeed the preparation of an artificial soil had to be resorted to in order to study the behaviour of the normal root. Apart from this portion of the tips of vigorous roots none were found free from endotrophic filaments.

The first sign of infection is the presence of a few filaments in the outer cortex, the cells of which are still hyaline. Later the threads spread throughout the cortex and the cells take on a brown colour. Filaments may be observed in all stages running over the epidermis. Their number gradually increases until a mantle is produced. This is usually present at the point of formation of endogenous lateral rootlets which must force their way through the mantle. In so doing a mantle grows around them and filaments penetrate the cells and the majority are destined to become mycorrhizas instead of lateral roots. It is not definite whether internal infection precedes the formation of the mantle in this case as well as that of the axial growing tip. Masui (1927) believes the converse to be true.

3. SITE DESCRIPTION.

For the sake of completeness a brief description of the plantation site—Block 3A Tinjella Tract, Kuitpo Forest, South Australia—where these observations were recorded, is included.

The original vegetation obtained from the forest records was *Eucalyptus viminalis* over *leptospermum sp.* and bracken fern. The plantation of *Pinus radiata* was established in 1903 with a spacing of 8 feet by 8 feet. It has been thinned and pruned and the mature stand at 30 years has a volume of 10,000 c.ft./acre, and an M.A.I. of 400 c.ft./acre/ann. including thinnings. The block has a gentle slope with a southerly aspect. All undergrowth has been fully suppressed, while the needle litter is about 1 inch thick.

The soil is of the Myponga Sand type (Taylor and O'Donnell (1932)) i.e., a podsolised sand over mottled sandstone, in this case at a depth of 40 inches.

A description of the surface horizon, a grey sand 0–4 inches in depth, follows—

Mechanical analysis (International System)—

Coarse sand	57.0
Fine sand	54.2
Silt	2.6
Clay	3.2
Loss on Acid Treatment	0.6
Moisture	1.3
Total	98.9
Loss on ignition	2.1

Characters—

P H	6.18
Volume weight	1.40
Field carrying capacity (Kopecky's method)	26.6 per cent. (volume)
Hygroscopic coefficient	1.7 per cent. (volume)
Air Dry Moisture Content	1.0 per cent. (volume)

Table of volumetric moisture content at 2 inches depth.

Date.	October.				November.			December.	
	10th.	16th.	23rd.	27th.	3rd.	16th.	27th.	6th.	19th.
Moisture	Per cent. 12.0	Per cent. 9.7	Per cent. 10.9	Per cent. 6.7	Per cent. 6.7	Per cent. 2.4	Per cent. 2.8	Per cent. 6.6	Per cent. 4.5

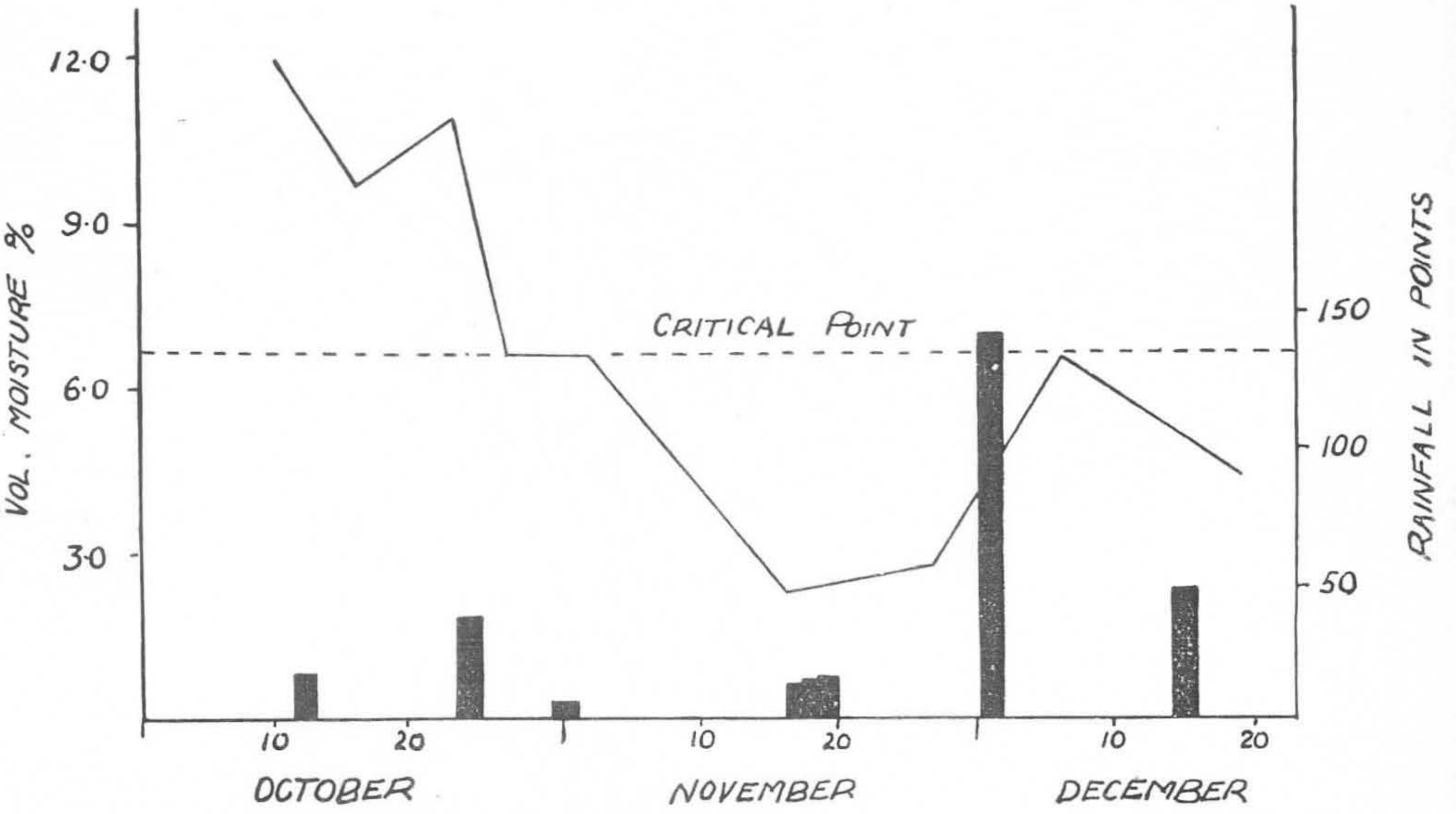
In spite of European experience the high P H value 6.18 is not unfavorable to the production of the mycorrhiza here considered.

The volumetric moisture content and the rainfall have been graphed against the period of observation, *see* Figure 1.

The first observation of the desiccation of the root tips occurred on 27th October, at a moisture content of 6.7 per cent. (volume). This value is approximately four times the hygroscopic coefficient and one quarter of the field carrying capacity.

Wilting point determinations with wheat seedlings were unsatisfactory and have not been included.

Figure 1.



Graphical representation of the soil moisture conditions of the surface horizon (0-4 inches) during the critical period.

V. THE ROOT UNDER DROUGHT CONDITIONS.

1. THE MOISTURE CONTROL OF GROWTH.

It is not necessary to labour the point that trees are wholly dependant upon a sufficient water supply. Among the complex of environment factors which govern plant growth, soil moisture frequently becomes limiting. This single factor then assumes control of the rate and amount of growth. The researches of MacDougal (1930) and Haasis (1932) on the growth of trees by means of the dendrograph have shown that trees are particularly sensitive to moisture conditions. Diurnal shrinkage and swelling due to desiccation and rehydration are recorded as well as seasonal fluctuations. The significance of soil moisture is pointed out particularly in relation to seasonal changes, and the fact that the advent of rain may check or reverse such changes. Further the continuous growth recorded for three years on a monterey pine was ascribed to the soil moisture conditions around its roots making wood formation possible.

An examination of the ultimate roots during periods of adequate moisture reveals that the vigorous tips are large, turgid and whitish in colour. *See* Plates III. and IV. During periods of deficiency the tips are shrunken, dried and brown, a fact which will be further considered below.

It is reasonable to suppose that this is due to soil drought rather than to temperature or change of season. Confirmation was obtained from observation, namely—

(1) When the great majority of root tips were already dormant those in sheltered situations with higher moisture content continued to function and remained turgid. When the soil dried out these too became dormant.

(2) The roots growing on the edge and into a trenched plot with a high moisture content continued unchanged in mid summer when the remainder had been dormant for two months.

(3) An artificial soil made by a high mound of sand which remained moist in the summer was filled with vigorous growing roots while the dry soil surrounding the mound was marked by the dormant condition of the roots within it.

2. THE STATE OF THE GROWING TIPS.

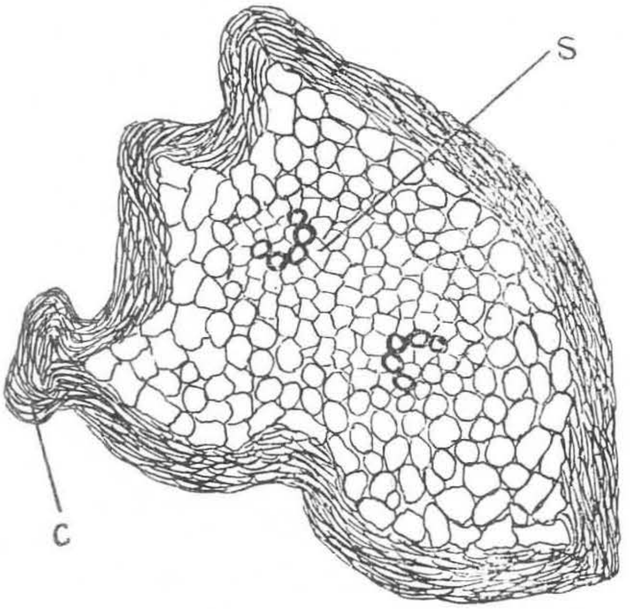
Microscopic examination reveals the nature of the shrinkage and drying up of the growing root. The cells of the cortex undergo a complete collapse and shrink together around the pericycle tissue. The desiccation is practically confined to the cortex which seems to form a protective layer around the vascular cylinder. The pericycle becomes slightly distorted to conform with the distortion of the cortical layer but little desiccation of the cells is visible. The state of the root tip at this stage is shown by Figure 2 and for comparison the root under normal conditions is given by Figure 3.

The difference between plasmolysis and permanent wilting has been pointed out by Maximov (1929). That the above effect is not merely loss of turgor is demonstrated by the inability of the cells to recover when immersed in water, and further by the collapse of the walls themselves.

It must be borne in mind that this distortion occurs before the development of a cork cambium to which the loss of the cortex is usually attributed. The cambium may form subsequently in the pericycle just below the layer of shrivelled cortex. It is, of course, formed in the normal way in roots which have not been subjected to drought conditions.

The shrivelling commences from the outside and advances inwards. All stages of cortical shrinkage may be found, from a few cells to the entire cortex according to the severity of the soil drought.

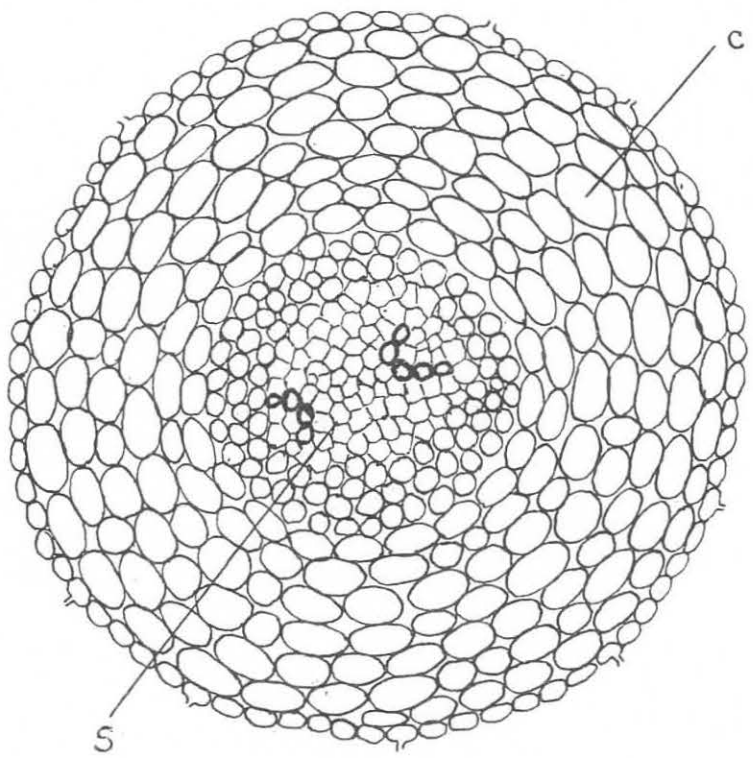
Figure 2.



ross section of root in the region of elongation under soil drought conditions.

S. Stele. C. Collapsed cortex.

Figure 3.



Cross section of root in the region of elongation under normal conditions.
C. Cortex. S. Stele.

3. The State of the Mycorrhizal Rootlets.

The mycorrhizal rootlets are already provided with a protective layer in the shape of the fungus mantle which surrounds the cortex.

Microscopic observation failed to detect any corresponding shrinkage or collapse in the cortex of the mycorrhizas. Desiccation of these rootlets therefore does not take place.

It is evident that the fungus is responsible for the protection afforded but whether this is due to the presence of the mantle, or to the ability of the fungal hyphae to absorb moisture at a lower moisture content than the normal root, remains to be elucidated.

The evidence suggests that the mycorrhizas are capable of enduring a higher degree of soil drought than the pine roots.

VI. THE EFFECT OF RAIN.

1. On the Dormant Roots.

The condition of the growing tips of the pine roots renders the response to moisture stimulus impossible. The root hairs have perished while the piliferous layer and cortex have collapsed so that absorption cannot take place. Maximov (1929) has stated " Evidently the roots are injuriously affected by drought considerably earlier than the leaves and under natural conditions a plant with desiccated roots, but still living leaves is doomed to perish ". This is the state which obtains (in the absence of mycorrhiza) in early summer when soil drought occurs.

The root system is essentially a shallow one. The majority of absorbing roots occur in the first 6 inches of soil and comparatively few penetrate deeper than 2 feet.

Heyward (1933) has described the root system of longleaf pine, its form consisting of—

(1) A prominent tap root.
(2) A set of horizontal lateral roots.
(3) A series of vertical roots descending from the laterals.

Mature *Pinus radiata* does not possess a tap root but corresponds in the remaining features. The vertical roots do not form minor laterals freely and rapidly decrease in thickness, i.e., do not usually penetrate to great depths. Heyward found that approximately 90 per cent. of the laterals occurred within a foot of the surface in deep sand. In this regard monterey pine is very similar.

From periodic measurements of site moisture content the writer has determined that soil drought occurs in the sandstone " C " horizon of the Myponga sand at a depth exceeding 3 feet 6 inches where pine roots in the penetrable sandstone are very scarce. Absorption from such a profile would be very small if it were possible at all.

During the summer and autumn of 1933 soil drought conditions prevailed until 14th April, which indicates a total period of over five months when normal water absorption is impossible. Even at the end of this period a re-organization of the absorbing system would have to take place before the intake of water could occur. The stimulus for the renewal of root growth would have to be given by some other means distinct from absorption, and in any case moisture would have to be supplied to the new tissue from some other source. This appears an insuperable condition for the tree is already in a state of water deficiency.

2. ON THE MYCORRHIZAL ROOTLETS.

It has been shown that the mycorrhizal rootlet is not shrivelled by conditions of soil drought, and should be capable of functioning. If this is so, the incidence of rain will render absorption possible immediately, and other conditions being suitable, will provide the means for growth.

Reference to the graph will show that the soil water had fallen to critical point by 27th October. No rain of any consequence fell until 1st December, when 140 points were recorded. It is unfortunate that the maximum point on the graph, viz., the content on 2nd December, was unable to be determined. There is no doubt that the value would have been above the critical point. Nevertheless the response to this precipitation was quickly demonstrated by the renewal of growth of the mycorrhizas. Within three days the mycorrhizal rootlets showed a swollen, turgid, whitish tip of new growth.

This renewal of growth has been observed and described by Masui (1926) but was not correlated with any special conditions, for example, of soil moisture.

Mycorrhizas in this condition have been photographed, Plates V. and VI.

The shrivelled dormant roots did not respond to this rain. However over a fortnight later after a further fall of 48 points a limited amount of new growth was made at the extreme end of some of these roots. The shrivelled portions remained in this condition and presumably the renewal of growth was due to the moisture afforded from the absorption by the mycorrhizal rootlets. Had this meant the continuance of moist soil conditions, instead of transitory, it is highly probable that new root hairs would have been formed leading to the intake of moisture in the ordinary way.

VII. DISCUSSION OF THE SIGNIFICANCE OF MYCORRHIZA.

The researches of Melin and Masui have shown that Boletus is not entirely nutritively parasitic. The utilization of certain salts is balanced by the supply of others, i.e., the fungus is a hemi symbiont.

With regard to the absorption of water it has been established that the fungus provides a ready channel. An endeavour has been made herein to show that under environmental conditions leading to soil drought—

(1) The absorbing tips of pine roots cease to function as such.
(2) Mycorrhizal rootlets do not adopt a dormant condition.
(3) The mycorrhizal root is capable of response to moisture supply.
(4) Stimulus for renewed growth is provided by the absorption of moisture by the mycorrhizas.

It is therefore suggested that the relationship is highly beneficial to the tree under environmental conditions comparable with those existing at Kuitpo. The writer hopes that this paper will stimulate interest in the subject and lead to further research along these lines.

VIII. SUMMARY.

1. The mycorrhiza of *Pinus radiata* is described.

2. The infection is attributed to the Basidiomycete, *Boletus granulatus*.

3. The mycorrhiza is shown to be ectendotrophic.

4. A description of the site under observation is given, including periodic soil moisture determinations.

5. Soil drought is shown to cause the collapse of the cortex of the absorbing roots of the pine, but not of the mycorrhizas.

6. The effect of moisture supply after soil drought is to renew the growth of the mycorrhiza.

7. It is suggested therefore that the symbiotic relationship is highly beneficial to the tree.

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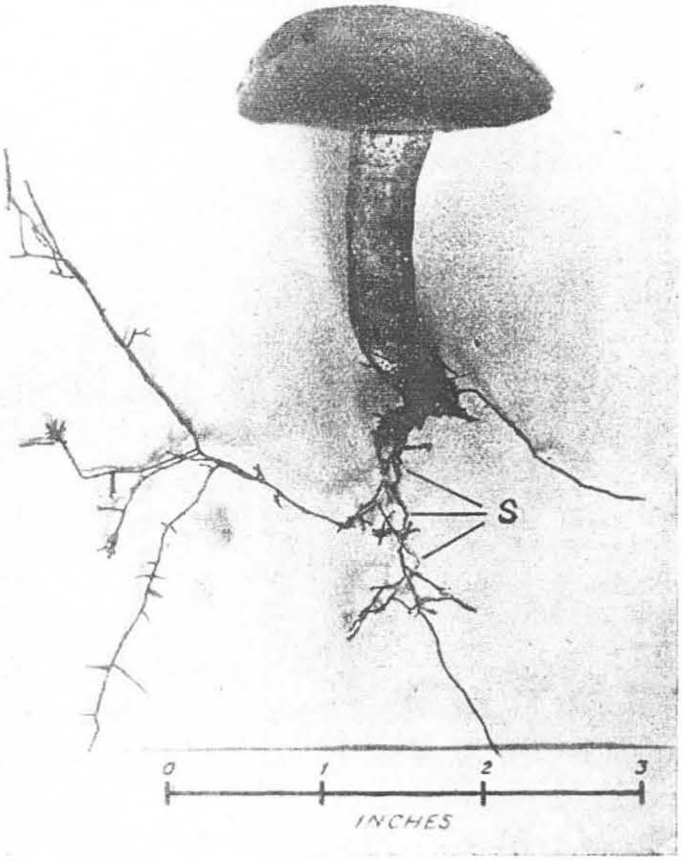
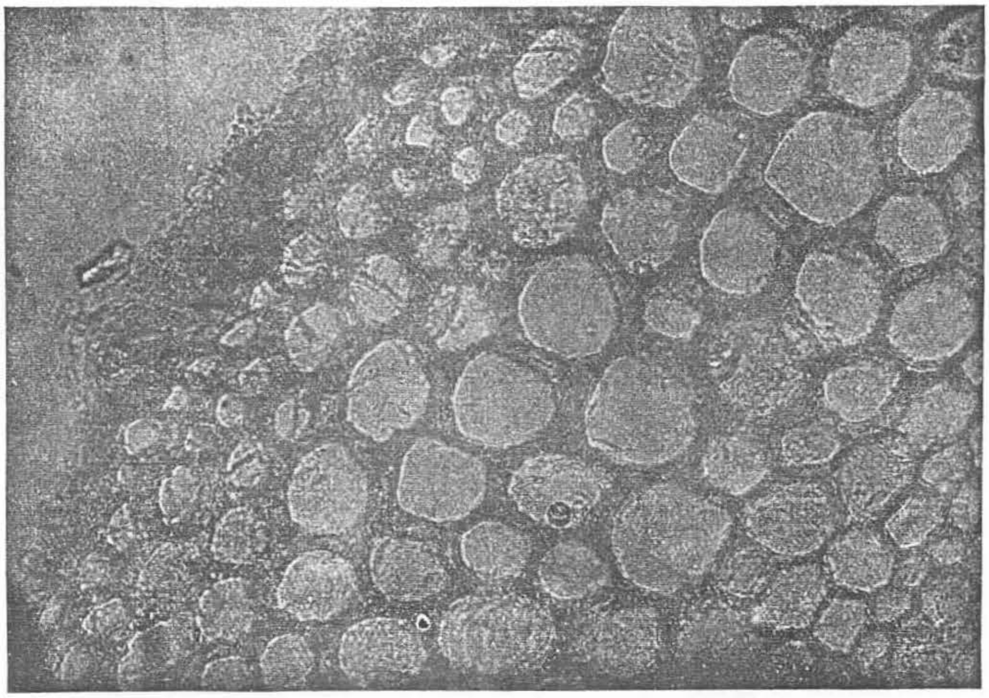
Plate 1.



A fruiting body of Boletus granulatus attached by hyphal strands to mycorrhizal roots of P. radiata.
S.—Hyphal Strands.

Plate 2.

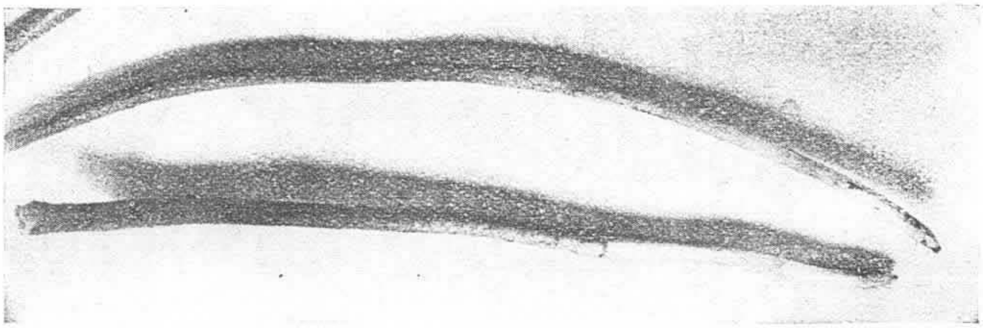


Portion of the cortex of a root showing the endotrophic filaments.
e. endotrophic filaments. m. portion of mantle.

Plate 3.

Root tips under moist conditions. The Layer of needles and the surface soil have been scraped away exposing the whitish absorbing tips.

Plate 4.



Showing the turgid state of the root tips under conditions of adequate moisture. Natural size.

Plate 5.

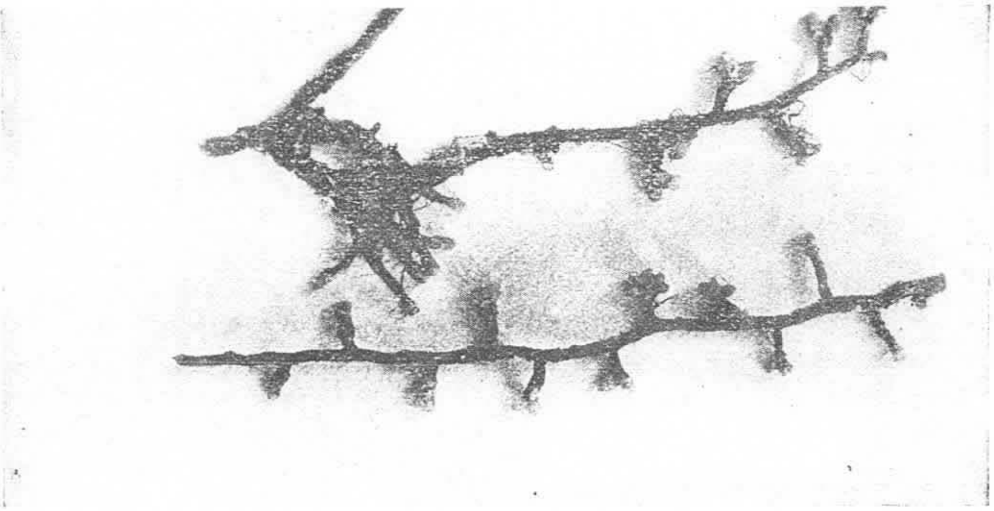
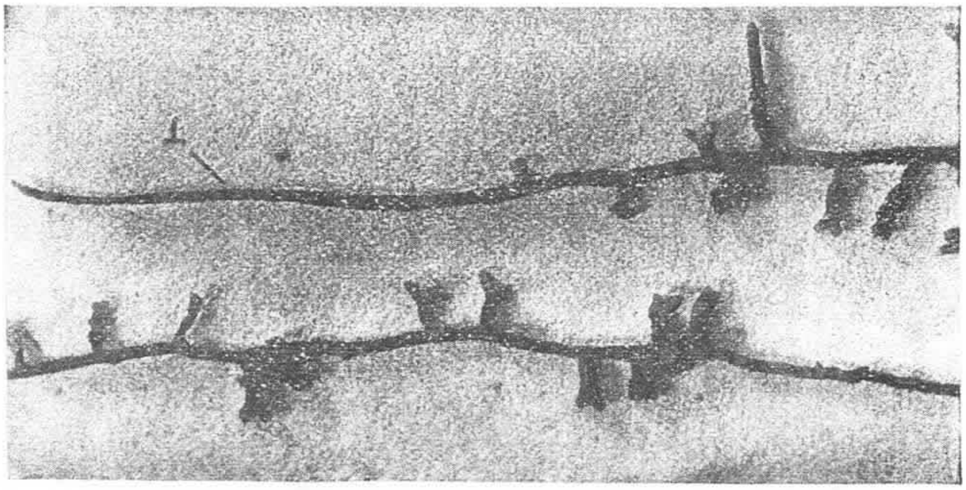


Plate 6.



Renewed growth of mycorrhizas after rain following soil drought. X 3. Note the dark shrivelled root tip. (T)

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